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The Relationship Between Primary Production and the Vertical Export of Particulate Organic Matter in a River-Impacted Coastal Ecosystem

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ABSTRACT: As part of the National Oceanic and Atmospheric Administration's (NOAA) Nutrient Enhanced Coastal Ocean Productivity program, we have conducted four research cruises, July–August 1990, March 1991, September 1991, and May 1992, in the Mississippi River plume and adjacent shelf regions. Over this time period, photic-zone-integrated primary production varied significantly in both the river plume and shelf study regions, with greatest variability observed in the river plume region. In the river plume and the adjacent shelf, highest production occurred during July–August 1990 (8.17 g C m^{-2} d^{-1} for the plume and 1.89–3.02 g C m^{-2} d^{-1} for the shelf) and the lowest during March 1991 (0.40–0.69 g C m^{-2} d^{-1} for the plume and 0.12–0.45 g C m^{-2} d^{-1} for the shelf). The vertical export of POC from the euphotic zone, determined with free-floating MULTITRAP sediment trap systems, also varied temporally in both study regions, with highest values occurring in May 1992 (1.80 ± 0.04 g C m^{-2} d^{-1} for the plume and 0.40 ± 0.02 g C m^{-2} d^{-1} for the shelf) and the lowest values occurring during July–August 1990 (0.29 ± 0.02 g C m^{-2} d^{-1} for the plume and 0.18 ± 0.01 g C m^{-2} d^{-1} for the shelf). The fraction of production exported out of the photic zone was highly variable and was dependent, in part, on phytoplankton species composition and on the grazing activities of microzooplankton and mesozooplankton. The lowest ratio of export to production coincided with the time when production was greatest and the highest ratios occurred when production was the lowest.

Introduction

The Mississippi River drains more than 40% of the continental United States. Over the past 35–40 yr there has been a twofold increase in the observed concentrations of NO_3^- measured in river waters near the modern "birdsfoot" delta (Turner and Rabalais 1991; Dinnel and Bratkovich 1993; Bratkovich et al. 1994). Examination of monthly records have led Dinnel and Bratkovich (1993) to conclude that seasonal variation in dissolved NO_3^- concentrations, which are superimposed on a generally increasing trend, are linked with seasonal trends in river discharge. Higher nutrient concentrations are associated with higher river discharge rates (e.g., in winter and spring). Conversely, low river discharge appears to be correlated with lower nutrient concentrations in the river waters. One consequence of river flow into the coastal Gulf of Mexico is the development of stratification, with a lower salinity layer overlying a more saline coastal seawater layer. This stratification and the development of salinity fronts has been related to observations of primary production with production enhanced along these salinity fronts (Lohrenz et al. 1990). It has been suggested that the trend of increasing dissolved inorganic nutrient concentrations could result in elevated levels of primary production in the coastal regions of the Gulf of Mexico (Sklar and Turner 1981; Lohrenz et al. 1990). Further, it has been suggested that the increased levels of primary production would give rise to increased sedimentation of particulate organic matter (POM) and possibly contribute to the frequently observed episodes of hypoxia on the inner Gulf shelf (Turner et al. 1987). One of the

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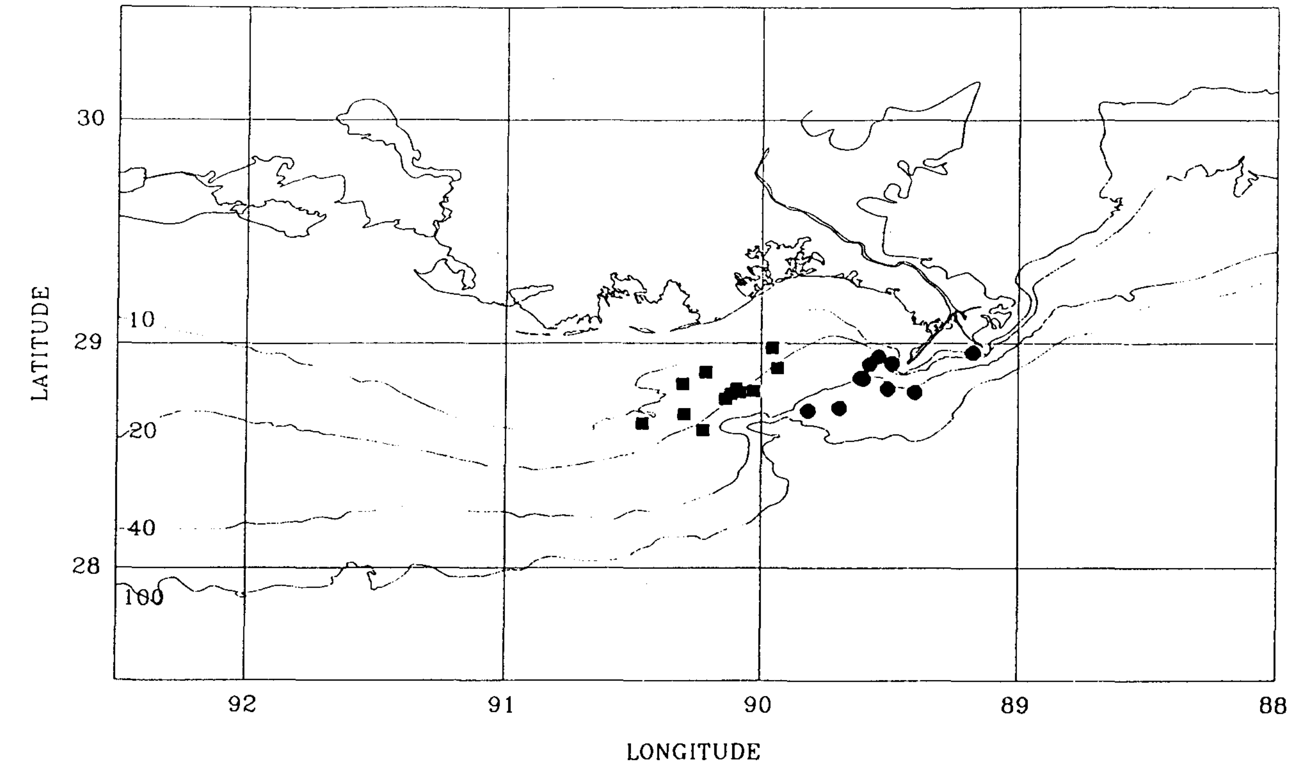

Fig. 1. The NECOP study has examined stations in the Mississippi River plume (filled circles) and in the adjacent shelf region (filled squares). Symbols indicated the location of primary production experiments associated with the free-floating sediment trap array deployments. Contour lines indicate the 10 fathom, 20 fathom, 40 fathom, and 100 fathom bathymetry.

objectives of our study has been to examine temporal variability in primary production relative to variations in river flow for two regions: the Mississippi River plume and the inner Gulf of Mexico shelf (cf. Lohrenz et al. 1992a, 1994). It is the goal of this continuing study to examine the temporal variability in the relationship between primary production and the export of POM from the euphotic zone in the study regions.

Materials and Methods

Research cruises were conducted in the study regions (Fig. 1) onboard the NOAA ship *Malcolm Baldrige* (cruise MB90079, July–August 1990 and cruise MB910304, March 1991) and the R/V *Pelican* (cruise PE910921, September 1991, and cruise PE920505, May 1992). The first of these cruises was conducted during a period usually considered a low river-flow season (July–August, 1990). However, the cruise was conducted following a period of heavy rains and conditions were not entirely consistent with usual low river-flow situations; observed stratification could be attributed to both vertical salinity and temperature gradients, rather than just due to thermal stratification. The second cruise was conducted during a high river-flow season (March, 1991). The remaining two cruises (September 1991 and May 1992) were conducted during low river-flow conditions. During each cruise, studies were conducted in the Mississippi River plume and the inner Gulf shelf to measure primary production at selected stations using 24-h simulated in situ incubations conducted in temperature, light quality, and light quantity controlled deck-top incubators (Lohrenz et al. 1990, 1992b). Also during each cruise, free-floating MULTITRAP sediment trap arrays (Knauer et al. 1979) were deployed, generally for 1–2 d, in both study regions to quantify the export of POM from the euphotic zone. The productivity experiments discussed here were coordinated with the sediment trap deployments; sunrise to sunrise production experiments were generally conducted on both days of each trap deployment.

For the productivity experiments, water samples were collected prior to sunrise using either acid-washed 10-l Niskin bottles (with silicone rubber tubing for bottle closure) or 10-l and 30-l acid-washed and teflon-lined Go-Flo bottles from three depths corresponding to the 50%, 12%, and 1% light depths. Light depths were determined from vertical profiles of photosynthetically available radiation (PAR), which was measured with a Biospherical Instruments PNF300 profiling natural fluorometer on the day prior to that on which production was to be measured. The three light depths chosen correspond to the light transmission characteristics of the simulated in situ on-deck incubation system (Lohrenz et al. 1990, 1992b). Samples were placed in 1-l polycarbonate bottles, inoculated with 250 μCi $H^{14}CO_3^-$ and incubated from sunrise to sunrise. Trace metal clean procedures, as recommended by Fitzwater et al. (1982), were employed in preparing incubation containers and isotope stock solutions throughout the study. Zero time blanks were used to correct particulate ^{14}C activities (Morris et al. 1971). Total inorganic carbon was analyzed for each productivity sample as described by Lohrenz et al. (1994). After the incubations were complete, replicate subsamples were filtered onto Whatman GF/F filters to determine particulate ^{14}C activity. Particulate ^{14}C activity filters were then placed into liquid scintillation vials containing 0.5 ml of 10% HCl, which removed residual $H^{14}CO_3^-$ (Lean and Burnison 1979). In most instances, postincubation size-fractionation techniques (using Poretics polycarbonate 8-μm filters) were employed on replicate productivity bottles to determine the production for that portion of the phytoplankton community that was <8-μm in diameter. Concurrent studies (Dortch et al. 1992; Fahnenstiel et al. 1992) have indicated that most of the diatoms present in our water samples would be retained on the 8-μm filter. Production of the <8-μm size fraction represents the activity of organisms that passed through the 8-μm filter (i.e., nondiatoms) and were subsequently collected on a GF/F filter. Subsamples were also taken to determine the total amount of $H^{14}CO_3^-$ added to each bottle by combining 0.5 ml of sample with 0.5 ml of a 50% (v/v) mixture of ethanol and ethanolamine. Sample ^{14}C activities were determined using SafetySolve liquid scintillation cocktail with a Packard Liquid Scintillation Analyzer.

Replicate (4–5) MULTITRAP sediment traps were attached to trap-holder crosses and deployed at 15 m on free-floating arrays for each study region on both cruises. In our study areas, a depth of 15 m was generally below the base of the euphotic zone but well above the bottom, thus minimizing contamination due to collection of resuspended materials. In all cases, a second set of sediment traps was deployed approximately 10 m below the trap at 15 m. The data from these traps will not be presented here but were used to confirm that resuspension was not important in evaluating the results from 15 m. Deployments were 1–2 d in duration. Prior to deployment, each sediment trap was filled with a brine solution (final density = 1.08 g kg^{-1}, to prevent loss of collected materials upon recovery) containing 2% (v/v) formalin as a preservative. The base of each trap tube was fitted with a 0.8-μm Poretics filter and a drain port. After recovery, the preserved brine solution with the collected POM was drained through this filter. The POM collected on the filters was examined microscopically to remove any "swimmer" zooplankton, which would contaminate the sample (Karl and Knauer 1989; Knauer et al. 1984; Lee et al. 1988). The collected POM was treated as described by Knauer et al. (1979) and concentrations of particulate organic carbon (POC) and particulate organic nitrogen (PON) collected in each trap were then determined using a Carlo Erba NA1500 Nitrogen-Carbon Analyzer.

Concentrations of chlorophyll *a* (chl *a*) were determined fluorometrically for samples filtered onto Whatman GF/F glass-fiber filters (Shoaf and Lium 1976). In addition, the concentrations of dissolved NO_3^-, PO_4^{3-} and SiO_3^- were determined using either Alpkem or Technicon autoanalyzers with the standard automated techniques (Whitledge et al. 1981).

Results

In the study region, a high degree of variability over time was observed in near-surface salinity, nutrient concentrations, and in the values of other environmental parameters, such as chl *a* concentrations, the mass of suspended particulate matter (SPM), and the average vertical extinction coefficient for PAR in the upper 5 m (K_{par}) (Table 1). For example, the surface concentrations of NO_3^- varied from near the lower limit of detection, 0.05 μM, to high values of 100 μM. Surface concentrations of PO_4^{3-} and SiO_3^- were also seen to vary over time but not to the extent observed for NO_3^-. Salinities ranged from 12.55‰ to 30.20‰ in the plume region and from 20.64‰ to 34.36‰ in the shelf region; the lowest values occurred during March 1991 and the highest during May 1992. Surface chl *a* concentrations varied by a factor of 10 during the study, with lowest values observed during March 1991 and September 1991 and highest values observed during July–August 1990 and May 1992.

The results of the productivity studies associated with the sediment trap deployments for each of the cruises are shown in Fig. 2 a–d, for the July–August 1990, March 1991, September 1991, and May 1992 cruises, respectively. For all of the experiments, the deepest sample was obtained from the 1% light depth, which is generally taken to represent the bottom of the euphotic zone. The 0.1% light depth was in most cases within 1 m of the 1% light depth for the plume stations and no more than a few

TABLE 1. Environmental characteristics of the surface waters in the Mississippi River plume and adjacent shelf study regions. Ranges are given for each parameter measured during the series of four research cruises conducted as part of the NECOP program.

Region	July–August 1990	March 1991	September 1991	May 1992
Surface Nitrate Concentrations (μM)				
Plume	30–100	10–31	0.05–0.65	16–42
Shelf	1.7–23.6	0.4–13.2	<0.02	0.5–5.0
Surface Phosphate Concentrations (μM)				
Plume	0.12–2.15	0.2–0.9	0.25–0.9	0.7–6.1
Shelf	0.05–2.15	0.3–0.38	<0.07	0.1–1.3
Surface Silicate Concentrations (μM)				
Plume	15.5–101	0.2–1.3	0.4–1.1	13.7–28.7
Shelf	0.4–3.5	<0.2–0.4	0.2	0.4–7.0
Surface Chlorophyll *a* Concentration (μg l^{-1})				
Plume	12.8–14.4	1.1–1.7	1.9–2.1	4.8–10.7
Shelf	10.1–11.8	0.3–0.8	0.03–0.2	2.8–7.3
Surface Suspended Particulate Matter (mg l^{-1})				
Plume	2.4–7.2	0.5–10.3	2.8–3.9	7.6–12.6
Shelf	0.9–5.7	0.3–1.8	1.7–4.1	2.2–5.7
Average K(PAR) Over Upper 5 m (m^{-1})				
Plume	0.36–0.84	0.45–0.67	0.35–0.47	0.64
Shelf	0.52–0.64	0.26–0.68	0.06–0.28	0.13–0.41
Surface Salinity				
Plume	25.36–27.15	12.55–18.33	24.50–29.67	26.40–30.20
Shelf	33.07–33.12	20.64–25.36	29.88–32.93	32.18–34.36

meters deeper for the shelf stations. In general, photic-zone-integrated primary production (IPP; Table 2) rates were up to an order of magnitude greater in the river plume than in the adjacent shelf waters. Only during the March 1991 cruise were IPP values comparable in both study regions. In each study region, IPP varied over time during the field portion of the project. In the river plume, IPP ranged from a low value of 0.40 g C m^{-2} d^{-1} during March 1991 to a value of 8.17 g C m^{-2} d^{-1} during July–August 1990, over 20 times greater than the lowest observed value. Similarly, IPP values for the adjacent shelf region varied with time from a low value of 0.12 g C m^{-2} d^{-1} in March 1991 to a value 30 times higher, 3.02 g C m^{-2} d^{-1}, during July–August 1990. The <8-μm components of the phytoplankton community were responsible for 50% to 66% of the total IPP in the Mississippi River plume and 40% to nearly 100% for the adjacent shelf waters during the course of the study. The patchy nature of the study region is further demonstrated by the results of production experiments for the shelf region during March 1991 and during May 1992 (Fig. 2b,d). On these occasions, IPP varied by more than a factor of 3 from day 1 to day 2.

The vertical export of POC and PON determined during the sediment trap deployments in the two study regions exhibited a high degree of variability both between the two regions and over time within each region (Table 3). The vertical flux rates of POC out of the photic zone were low during the July–August 1990 cruise and high (approximately sixfold greater than July–August 1990) during the May 1992 cruise. Over the course of the field program, the vertical export of PON varied to a much lesser extent than POC export. As was the case for the vertical export of POC, the lowest export of PON was observed during July–August 1990 and the highest (approximately twofold greater) during the May 1992 cruise.

Comparison of the vertical export of POC from the photic zone in both the river plume and shelf regions to measured primary production on each day of the trap deployments shows that the fraction of production exported from the surface varied widely over the study period. During July–August 1990, a relativley small portion of the IPP (2.9–9.0%) was collected in the sediment traps, while a much larger portion (64–266%) of the IPP was collected in the traps in March 1991.

It is instructive to examine the relationship between the export of POC and PON from the photic zone and the various environmental parameters, such as IPP, the near-surface salinities and concentrations (average values for the upper 1–2 m) of NO_3^-, PO_4^{3-}, SiO_3^-, and chl *a*, the mass of SPM, and K'_{par} in the upper 5 m. It is important to determine the degree of interrelationship among these data in order to assess the impact of each parameter on the observed rates of primary production and the vertical export of POM to the shelf sediments. The Pearson Correlation was used to relate the mean values of the data to the environmental variables presented in Table 1. The correlation matrix values (n = 8 and df = 6 for each variable) are presented in Table 4. All values of r greater than 0.707 are considered significant ($p < 0.05$; Steel Torrie 1980). IPP is positively correlated with the near-surface concentrations of NO_3^-,

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Fig. 2. Simulated in situ primary production experiments conducted during the research cruises in the Mississippi River plume and the adjacent shelf region. Postincubation size fractionation studies were conducted to determine the production of the <8-μm components of the phytoplankton community. Symbols used are defined in each figure. Primary production profiles are given for the July–August 1990 (a), March 1991 (b), September 1991 (c; squares represent data from day 1 and circles represent data from day 2), and May 1992 (d) NECOP cruises.

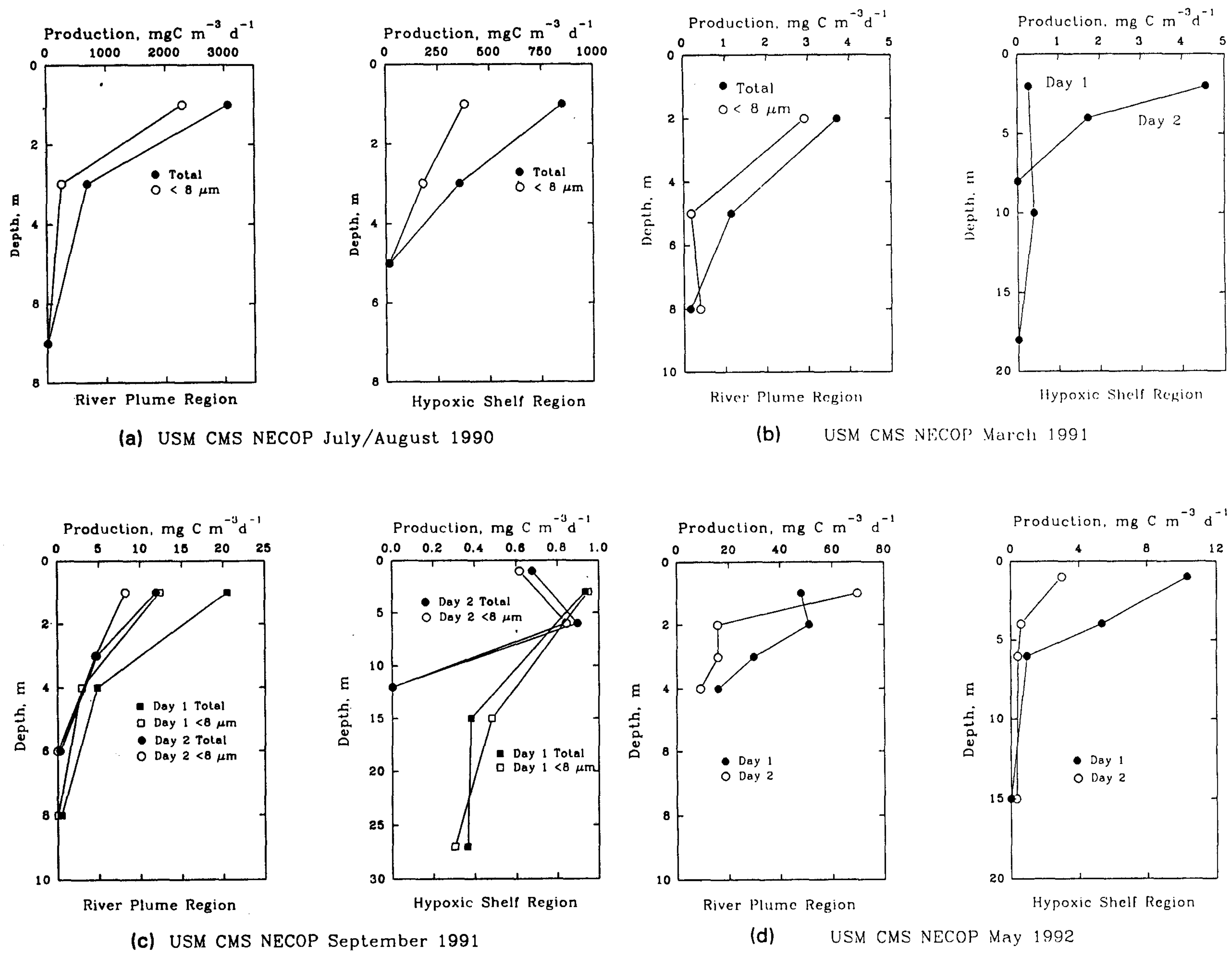
Production, mgC m-3 d-1
Depth, m
Total
< 8 μm
River Plume Region
Hypoxic Shelf Region
(a) USM CMS NECOP July/August 1990
Production, mg C m-3 d-1
Total
< 8 μm
Day 1
Day 2
River Plume Region
Hypoxic Shelf Region
(b) USM CMS NECOP March 1991
Day 1 Total
Day 1 <8 μm
Day 2 Total
Day 2 <8 μm
River Plume Region
Hypoxic Shelf Region
(c) USM CMS NECOP September 1991
Day 1
Day 2
River Plume Region
Hypoxic Shelf Region
(d) USM CMS NECOP May 1992

TABLE 2. Photic-zone-integrated primary production (IPP; g C m^{-2} d^{-1}) for the simulated in situ primary production experiments conducted on each cruise in both the river plume and adjacent shelf study regions. Values are given for those experiments associated with the free-floating sediment trap array deployments. In addition IPP results for the whole phytoplankton population and for the <8-μm size fraction determined with postincubation size fractionation procedures are presented. n.d. = no data.

	Integrated Primary Production			
	Plume Region		Shelf Region	
Cruise	Total	<8 μm	Total	<8 μm
July–August 1990	8.17	5.32	1.89–3.02	1.13
March 1991	0.40–0.69	0.27	0.12–0.45	0.11
September 1991	0.86–1.65	0.67–0.99	0.17–0.36	0.16–0.39
May 1992	3.37–3.86	n.d.	0.28–1.07	n.d.

TABLE 3. Vertical flux of particulate organic carbon (POC) (g C m^{-2} d^{-1}) and particulate organic nitrogen (PON) (g N m^{-2} d^{-1}) out of the photic zone for the four NECOP cruises completed thus far. The standard error and number of replicate samples are given in parentheses.

Cruise	Plume Region	Shelf Region
July–August 1990		
POC Flux	0.29 (0.02; n = 3)	0.18 (0.01; n = 4)
PON Flux	0.06 (0.003; n = 6)	0.03 (0.002; n = 8)
March 1991		
POC Flux	0.95 (0.01; n = 3)	0.32 (0.02; n = 3)
PON Flux	0.16 (0.009; n = 6)	0.05 (0.002; n = 6)
September 1991		
POC Flux	0.69 (0.02; n = 12)	0.19 (0.01; n = 6)
PON Flux	0.12 (0.003; n = 12)	0.03 (0.001; n = 6)
May 1992		
POC Flux	1.80 (0.04; n = 8)	0.40 (0.02; n = 10)
PON Flux	0.27 (0.008; n = 16)	0.07 (0.004; n = 10)

SiO_3^-, and chl *a*. The vertical export of POC and PON were significantly correlated. Additionally, both parameters were correlated ($p < 0.05$) with the near-surface concentrations of PO_4^{3-} and SPM. NO_3^- concentrations were correlated significantly with chl *a* and with the concentrations of the other nutrients with the exception of PO_4^{3-}. Using the model II geometric mean, least squares linear regression (Laws and Archie 1981), we also examined the relationship between the export of POC and PON and the mass of SPM in the river plume and adjacent shelf dataset. The linear regression analysis indicated that both POC and PON export were significantly related to SPM concentrations ($r^2 = 0.80$, $p < 0.05$, Eq. 1 and $r^2 = 0.80$, $p < 0.05$, Eq. 2, respectively).

$$POC_{export} = -0.02 + 0.21[SPM] \quad (1)$$

$$PON_{export} = -0.04 + 0.03[SPM] \quad (2)$$

Discussion

It appears that the rates of primary production, the vertical export of POM from the photic zone, and the relationship between IPP and the export of POM vary over time in both study regions in a complex manner. Conventional wisdom suggests that higher levels of IPP should be associated with higher rates of vertical export of POM from the photic zone (Eppley and Peterson 1979; Walsh et al. 1989). The observations discussed by Eppley and Peterson (1979) were derived, in general, from both coastal and open ocean environments using short-term measurements of primary and new production. The descriptive model presented by Walsh et al. (1989) for the continental margins in the Gulf of Mexico relies on the conceptual framework suggested by Eppley and Peterson (1979). One would expect then, based on these treatments, that the vertical export of POC would average 35–50% of IPP in our study region in the northern Gulf of Mexico. Our results, however, do not show any clear trends in the relationship between POC export and IPP. If one compares the data presented in Table 2 for IPP and Table 3 for the export of POC, it is clear that the ratio of export to POC varies from low values of 3–9% during July–August 1990 to high values during March 1991, when export exceeded measured IPP by a factor of about 2. In contrast, there appears to be a strong relationship between the input of dissolved NO_3^- and SiO_3^- from the outflow of the Mississippi River and the observed rates of IPP as is seen in the significant correlation of these parameters (Table 4). The increases in riverborne anthropogenically derived nutrients observed over the past several decades (cf. Dinnel and Bratkovich 1993; Bratkovich et al. 1994) appear to have contributed significantly to high rates of generation of POM and chl *a*. It is clear that greater temporal coverage (e.g., more frequent observations) would be necessary before any conclusive relationship between rates of IPP and POC export can be derived. Our data are not sufficient to conclude that the higher rates of IPP we observed have resulted in a greater flux of POM to the shelf sediments and thus, contributed to the periodic episodes of hypoxia. This observation is reinforced by the results of correlation and regression analyses, which indicated that the export of POC and PON were correlated significantly with both the mass of SPM and the near-surface concentrations of PO_4^{3-} rather than with IPP (Table 4). Indeed, it would be possible to relate the export of both POC and PON to measurements of just SPM in the regions studied (Eqs. 1 and 2). It is also interesting to note that near-surface concentrations of PO_4^{3-} were highly

TABLE 4. The Pearson Correlation matrix for mean values of selected rate processes (integrated primary production, IPP; vertical export of POC, F_{POC}; vertical export of PON, F_{PON}; surface concentrations of NO_3^-, PO_4^{3-}, SiO_3^- and chl *a*; mass of suspended particulate matter, SPM; diffuse attenuation coefficient over photosynthetically available radiation, K_{PAR}; surface salinity, SAL; units are the same as in Table 3). Correlation coefficient values which exceed 0.707 (six degrees of freedom) are considered to be significant at the 5% level.

	IPP	F_{POC}	F_{PON}	NO_3^-	PO_4^{3-}	SiO_3^-	Chl *a*	SPM	K_{PAR}	Sal
IPP	1.000									
F_{POC}	0.068	1.000								
F_{PON}	0.091	0.996*	1.000							
NO_3^-	0.934*	0.163	0.192	1.000						
PO_4^{3-}	0.397	0.832*	0.802*	0.375	1.000					
SiO_3^-	0.968*	0.073	0.099	0.948*	0.349	1.000				
Chl *a*	0.865*	−0.008	−0.001	0.748*	0.433	0.753*	1.000			
SPM	0.387	0.883*	0.881*	0.440	0.900*	0.376	0.362	1.000		
K_{PAR}	0.576	0.471	0.484	0.661	0.576	0.468	0.591	0.506	1.000	
Sal	0.068	−0.029	−0.338	−0.233	0.114	−0.011	0.335	−0.065	−0.401	1.000

correlated to export while the other nutrients measured during the study were highly correlated to IPP. Although we do not have sufficient data to make a definitive statement, it does appear that PO_4^{3-} cycles in the river plume and shelf regions are much different than those for either NO_3^- or SiO_3^-.

The use of free-floating sediment traps in a relatively shallow coastal system is often viewed with concern (Knauer and Asper 1989). It is possible that due to hydrodynamic complications, materials collected in the traps may not accurately reflect either the quality or quantity of the POM sinking to the shelf seafloor. There are several pieces of supporting evidence derived from other NECOP investigators that suggest that we did obtain realistic samples of sinking POM and can expect that the fluxes we calculated reflect flux rates characteristic of the study region. An additional concern is that the material collected in the traps is more representative of resuspended sediments than the material sinking through the water column. The stable isotope studies of Eadie et al. (1994) suggest, on the basis of $\delta^{13}C$ studies, that the material collected in the traps is marine in origin and is indistinguishable from that suspended in the water column. It is equally clear that riverborne suspended POM of terrigenous origin does not make a significant contribution to our trap-collected material; sediment trap POC $\delta^{13}C$ values reflect the characteristics of water-column POC in the region of highest observed IPP. One other concern is that material which has been resuspended from the sediments, with presumably similar $\delta^{13}C$ characteristics as exhibited by particles suspended in the water column, would be included in measurements of trap-collected POC. Although we have not presented the results here, the mass of POC collected in our deeper traps (see Materials and Methods) was always less than that we measured in the traps placed at 15 m, near the base of the euphotic zone. For this reason, we do not believe that resuspension of material presents any significant contribution to our export measurements.

Several researchers have examined the biases of sediment-trap collections in turbulent flow regimes (Butman 1986; Baker et al. 1988). From the results of these studies, it has been suggested that flow velocities near the trap mouth, relative to those of the array, on the order 12 cm s^{-1} or less will not adversely affect collection efficiency for cylindrical traps such as those employed in this study. However, flow regimes greater than 30 cm s^{-1} may seriously impact sediment-trap collection efficiencies. It is unclear what effect velocities in the 12–30 cm s^{-1} would have on collection efficiencies. The results from a related study conducted in the Mississippi River plume and shelf regions may provide information on trap efficiencies that would support the values we obtained in this study (Li et al. in preparation). Li et al. (in preparation) utilized a ship-mounted acoustic Doppler current profiler (RD Instruments, 600 kHz) to obtain estimates of current velocities near the surface and at the depths of the sediment traps. This was accomplished by conducting a series of transects both along and across the path of the trap array during deployment. A strong north wind front passed through the sampling region during their trap deployments resulting in surface current velocities that averaged greater than 50 cm s^{-1}. Since the winds which occurred during the NECOP study never reached the velocities measured during the Li et al. project, it is expected that relative to the NECOP results, this would be a "worst case" comparison. For the Li et al. study, the difference in current velocities between currents at the depth of the traps and that of the trap array averaged 20 cm s^{-1}. Thus the average flow regime at a trap mouth during their study was well below the value of 30 cm s^{-1}, which is associated with inefficient trap collections. A second study, conducted in the same region as our cruises, utilized a similar MULTITRAP system as was used here (Asper personal communication). In the Asper study, an electromagnetic current meter (Woods Hole Instrument Systems) was placed in-line in the trap array at the same depth as the individual sediment collectors. Results of this deployment indicated that relative current flows at the trap depths were on the order of 4 cm s^{-1}. Weather conditions were similar to those encountered on our series of research cruises (Asper personal communication). It is likely, therefore, that during the studies presented here, the current velocity at trap mouth depths relative to that of the array would be well within the range where we would expect no adverse effects on sediment-trap collection efficiencies (cf. Knauer and Asper 1989).

It appears that our July–August 1990 cruise may have been at variance with long-term average conditions for summer (cf. Dinnel and Bratkovich 1993) in that our cruise was preceded by a period of higher than normal river discharge with concentrations of NO_3^- > 20 μM in the river plume. These conditions resulted in a highly stratified water-column in both the plume and shelf regions, and gave rise to the highest values of IPP and the lowest ratios of POM export to IPP observed in the study. Some of the environmental conditions measured during the March 1991 cruise were similar to those measured during July–August 1990 (Table 4). It should be noted that the water column during March 1991 was stratified due to the high river flow at that time and that incident PAR and surface concentrations of both SiO_3^- and chl *a* were lower than during the previous cruise. During March 1991, we obtained the lowest values of IPP and the highest ratios of POM export to IPP observed during the study. It is clear that the parameters impacting IPP are different from those leading to the vertical export of POC and PON.

Temporal variation in the irradiance field combined with the absorption and scattering properties of the dissolved and suspended materials in the plume and shelf areas may contribute to the observed variation in primary production (Lohrenz et al. 1990, 1992a, 1994). Yet Lohrenz et al. (1994) were able to show that variability in environmental conditions could only explain part of the observed variation in photosynthetic-irradiance parameters (i.e., α^B and P^B_{max}). The differences in the ratio of the vertical POC flux to IPP cannot be explained solely on the basis of differences in IPP resulting from heterogeneity in the physical and chemical environment. It appears that at least three additional factors would likely contribute to temporal differences in the fraction of the organic matter produced in the photic zone which is exported to the sediments: differences in phytoplankton communities present, differences in the activities of both microzooplankton and macrozooplankton grazers, and horizontal advection of particulates into or out of the study regions.

We do not have any information available on the advection of water through our study areas. However, we can address the other two potential sources of variability. Our data suggest that those >8-μm components of the phytoplankton community, primarily diatoms, were of lesser importance than smaller organisms in their contribution to IPP for the river plume region. During both the July–August 1990 and March 1991 cruises, >8-μm size fraction was responsible for more than half of the IPP for the shelf region. However, during the September 1991 cruise, the <8-μm size fraction was responsible for virtually all of the IPP. It is interesting to note that more diatoms, principally *Skeletonema costatum,* were found in the sediment traps deployed in the plume than in those deployed in the shelf region during the July–August 1990 cruise (Dortch et al. 1992; Fahnenstiel et al. 1992). It is possible that the lower salinity and higher nutrient concentrations observed in the plume by Lohrenz et al. (1992a, 1994) may have contributed to diatoms being more important in the material collected in the plume sediment traps than for those deployed in the shelf region.

Zooplankton grazing activity is another factor that helps explain the observed differences in the proportion of the POM produced in the photic zone which is exported to the sediments. One would expect that grazing by macrozooplankton would be dominant in a coastal environment such as that examined here (Ortner et al. 1989).On each of the cruises, dilution experiments were used to examine the grazing activity of microzooplankton (Landry and Hassett 1982; Dagg and Ortner 1992; Fahnenstiel et al. 1992). Results suggest that microzooplankton grazing, which resulted in more tightly coupled production and regeneration of POM, was more intense during July–August 1990 than in March 1991. Our POM export results support this suggestion in that the fraction of IPP exported to the sediments was much lower when intense microzooplankton grazing was observed. The results of Benner et al. (1992) and Gardner et al. (1994) also support the greater regeneration of organic matter during July–August 1990 than in March 1991. Their bacterial production studies indicate that regeneration rates were an order of magnitude greater in the summer than in the following winter. Conversely, when macrozooplankton grazing activity was more intense (e.g., March 1991), rates of bacterial regeneration were much lower (Benner et al. 1992; Dagg and Ortner 1992).

It seems likely that decreased regeneration by bacteria and lower rates of microzooplankton grazing allowed for a larger portion of the IPP to be exported from the photic zone, as is seen in our sediment trap results. We suspect that for the September 1991 and May 1992 cruises, both bacterial activity and microzooplankton grazing activities were moderate because approximately half of the POC produced in the photic zone was exported to the sediments. This is consistent with the standard viewpoint of export production relative to primary production in coastal regions (Eppley and Peterson 1979; Walsh et al. 1989).

Conclusions

Our data from the NECOP program studies in the Mississippi River plume and the inner Gulf of Mexico region suggest that during July–August 1990, the production and regeneration of POM within the photic zone were tightly coupled, giving rise to a low rate of POM export to the sediments. Conversely, during March 1991, photic-zone production and regeneraton were relatively uncoupled, allowing for a greater fraction of the IPP to be exported from the photic zone. During September 1991 and May 1992, production, regeneration, and zooplankton grazing may have roughly been in balance such that about half of the IPP was exported out of the photic zone. Differences in phytoplankton species composition also contributed to the variability in the ratio of POM export to IPP. There appears to be no clear relationship between observed rates of IPP and export of POM from the photic zone; each parameter exhibited heterogeneity in both time and space throughout the study. Rates of IPP appeared to be a function of NO_3^-, SiO_3^-, and chl *a* concentrations, and thus river discharge, while POM export appears to be related to the mass of SPM and the concentrations of PO_4^{3-} rather than to any of the rate processes measured during this study.

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